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The architecture of human kin detection

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Evolved mechanisms for assessing genetic relatedness have been found in many species, but their existence in humans has been a matter of controversy. Here we report three converging lines of evidence, drawn from siblings, that support the hypothesis that kin detection mechanisms exist in humans. These operate by computing, for each familiar individual, a unitary regulatory variable (the kinship index) that corresponds to a pairwise estimate of genetic relatedness between self and other. The cues that the system uses were identified by quantitatively matching individual exposure to potential cues of relatedness to variation in three outputs relevant to the system's evolved functions: sibling altruism, aversion to personally engaging in sibling incest, and moral opposition to third party sibling incest. As predicted, the kin detection system uses two distinct, ancestrally valid cues to compute relatedness: the familiar other's perinatal association with the individual's biological mother, and duration of sibling coresidence.

For the past 50 years, evolutionary biologists have argued that genetic relatedness should have played a role in the social evolution of species, such as humans, in which close genetic relatives frequently interact[1,2]. According to kin selection theory, computational variants that allocate altruistic effort effectively with respect to kinship outcompete variants that fail to regulate behaviour conditionally in response to relatedness. The effects of relatedness have been documented in a great diversity of taxa, ranging from social amoebas[3], social insects[4–6] and shrimp[7], to birds[8], aphids[9], plants[10,11], rodents[12] and primates[13–15]. To regulate behaviour conditionally in response to different degrees of kinship, organisms require mechanisms to discriminate genetic relatedness. Such mechanisms have been discovered in a variety of nonhuman species[16–18].

Equally, in long-lived, low-fecundity species with an open breeding structure (such as humans), the fitness of offspring is strongly affected by how closely parents are related. In such species, conceptive sexual behaviour between close genetic relatives produces offspring that suffer from inbreeding depression—a decline in fitness caused by rendering more deleterious recessives homozygous[19–21], and aggravated by parasites targeting more genetically homogeneous sets of hosts[22,23]. Consequently, heritable variants that cost-effectively reduce inbreeding depression by avoiding mating with close genetic relatives outcompete variants in which mating decisions are unaffected by relatedness.

The socioecology and population biology of human foragers[24–26] suggest that our ancestors would have been subject both to inbreeding depression and kin selection. This leads to the prediction that humans have an evolved system for detecting genetic relatedness, coupled to two output systems: one regulating altruism, the other regulating mate choice. Yet, there has been little research into the existence and design of human kin detection mechanisms[27–32].

The best-known exceptions are a handful of anthropological studies testing Westermarck's prescient 1891 hypothesis[33] that mutual exposure during childhood weakens sexual attraction among adults. These documented that non-relatives raised together in exceptional developmental circumstances (for example, crèche-mates or children cohabiting with future spouses) show lower rates of marriage or marital fertility, and higher rates of divorce and infidelity—archivally derived sociological measures used as proxies for the intensity of sexual desire[34,35]. But to map the information-processing architecture of a system predicted to detect genetic relatedness—and see whether it regulates altruistic as well as sexual motivation—it is necessary to measure the responses of living individuals drawn from a more species-characteristic range of family compositions, such as those that include actual genetic relatives.

Accordingly, the goal of the studies reported here was to test for the existence of a human kin detection system, and to test a series of basic predictions about its design features and architecture. It is ethically unacceptable to subject humans to the life-changing experimental manipulations used to discover kin detection systems in other species. So the architecture was mapped by quantitatively matching individual variation in the two predicted output systems—sibling altruism and opposition to incest—to naturally generated individual variation in developmental parameters that were predicted to serve as cues of relatedness.

Model of architecture and predictions

We propose that, for each familiar individual, *i*, the kin detection system computes and updates a continuous variable, the kinship index, KI_i, that corresponds to the system's pairwise estimate of genetic relatedness between self and *i*. These computational elements are regulatory variables that serve as input to neural programs regulating altruism towards *i* and, separately, to programs regulating sexual behaviour towards *i*.

Because relatedness cannot be directly observed, the system must be designed to register cues relevant to determining relatedness. To compute the kinship index, the system requires (1) monitoring circuitry designed to register cues to relatedness, and (2) a computational device, the kinship estimator, whose procedures have been tuned by a history of selection to take these registered inputs and transform them into a kinship index.

The cues the system uses cannot simply be derived ontogenetically ('learned') by identifying which arbitrary and transient cues happen to best predict relatedness in the local environment. To do this, the system would have to already know the relatedness of others—the very problem it needs to solve. Instead, the kin detection system must contain within its evolved design a specification of the core cues that it will use to determine relatedness—cues that reliably tracked genetic relatedness in the ancestral social environments that selected for the kin detection system.

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For human foragers, a potentially informative cue to kinship is provided by the close perinatal association between mother and neonate that begins with birth and is enforced by the exigencies of early mammalian maternal care. Maternal perinatal association (MPA) provides a basis for the reliable mutual detection of mother and offspring and can, in turn, be used as an anchor point for sibling detection. Ancestrally, if an individual observed an infant in a durable, perinatal association with the individual's mother, then it was highly probable that that infant was the individual's sibling. We therefore proposed that sibling detection includes a monitoring subsystem specialized for registering MPA.

Although MPA is likely to be the single most informative cue, it cannot be used (for example) by younger siblings, because they are not alive at the time their older siblings are born and nursed. When MPA is unavailable, the kinship estimator should fall back on other cues that were highly predictive ancestrally. We predicted that the kin detection system would include a second subsystem specialized for registering the cumulative duration of coresidence summed over the full period they receive parental care. Ancestrally, parents (especially mothers) maintained close association with their children to care for them, and for this reason siblings co-associate statistically more than non-siblings. (Indeed, given the fusion–fission pattern of hunter–gatherer association, this same variable should—to some extent—link progressively more distant genetic relatives to increasingly diluted motivational residues.) Among human foragers, the maintenance of parental proximity for care delivery begins with birth and tapers off in late adolescence, a time when offspring become nearly independent adult foragers and when mating motivates new patterns of co-association[36,37]. Although this hypothesis differs from the ethological proposal of a period of early childhood imprinting[35], it is consistent with evidence that suggests that familiarity is a cue mediating kin detection in non-human primates[14,15,38,39].

The kinship estimator consists of algorithms for transforming the registered cues into the kinship index, a variable whose magnitude tracks relatedness between self and other. If the cues are integrated into a single index, then we should find that the same patterns of inputs are associated with the same patterns of outputs for both altruism and sexual aversion. This model (summarized in Fig. 1) leads to the following predictions.

(1) When MPA is absent, coresidence duration before adulthood with an individual should (a) upregulate altruism towards that individual, (b) upregulate sexual aversion towards that individual, and, as a by-product, (c) upregulate moral opposition[28,29] to third-party sibling incest.

(2) When MPA is present, it should produce the same three effects.

Selection should have tuned the procedures in the kinship estimator to use MPA and coresidence in a way that takes account of their relative informativeness and availability. Because MPA is the more robust, higher quality cue, we expect that when both are available, coresidence will be weighted by the kinship estimator far less than MPA, and perhaps not at all. Therefore, we propose a third prediction.

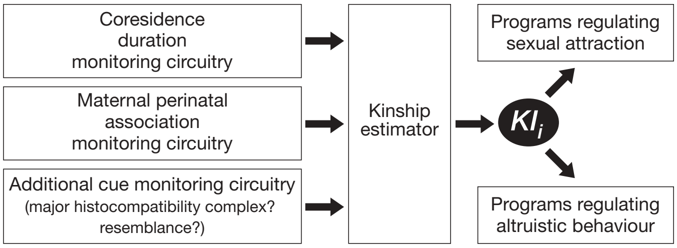

Figure 1 | Proposed model of the computational architecture of sibling detection. Cues to kinship are registered by cue monitoring circuits, which deliver their outputs to a kinship estimator. The kinship estimator uses these cues to compute the magnitude of a regulatory variable—a kinship index—for each individual, *i*, who is a potential sibling. The kinship index feeds into programs that regulate sibling altruism and sexual aversion.

(3) When MPA is present, coresidence duration will not be as strong a predictor of altruistic motivations and sexual aversions. That is, the kinship estimator will use MPA in preference to coresidence duration in computing kinship.

Empirical investigation

Multiple, converging tests involving over 600 subjects were employed to assess whether particular developmental parameters (including MPA and coresidence duration) serve as cues to kinship and regulate both kin-directed altruism and sexual avoidance. Participants responded to questions regarding family composition and sibling interactions and were asked to complete instruments measuring: (1) frequency of altruistic behaviours towards a given sibling; (2) the intensity of altruistic motivation towards a given sibling; (3) the level of disgust evoked by the prospect of engaging in sexual acts with a given sibling, and (4) how morally wrong they perceive sibling incest among third parties to be (an unobtrusive measure of sexual aversion towards siblings[28,29]).

Results

The most important findings are displayed in Figs 2 and 3, which show that each of the two predicted cues of genetic relatedness for siblings—coresidence duration and maternal perinatal association—regulate outputs from the two functionally independent motivational systems (altruism and incest aversion) in the predicted way. (see Supplementary Information section 1).

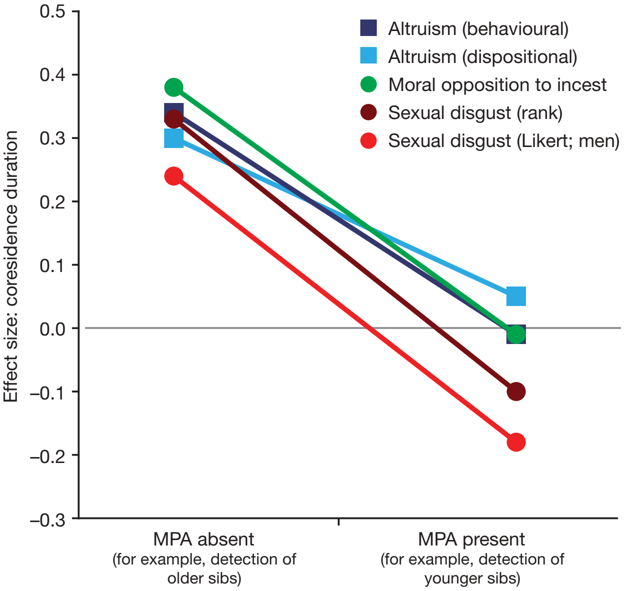

Figure 2 | Converging evidence indicates that the same computational variable, the kinship index, regulates disparate kin-relevant behaviours. The *x*-axis divides subjects into two groups—those who observed their mothers caring for their sibling as a neonate (MPA cue present) and those who did not (MPA cue absent). The *y*-axis shows the size of the correlation between coresidence duration and each dependent measure. Duration of coresidence predicts, with similar effect sizes, altruism and sexual aversions only when the cue of maternal perinatal association (MPA) is absent, as it is when younger siblings are detecting older ones. When the MPA cue is present, coresidence duration fails to predict sibling directed behaviours. This pattern appears for all measures: behavioural altruism, dispositional altruism, sexual disgust and moral judgments of sibling incest. Adaptive regulation of two distinct motivational output systems by the same pattern of inputs implicates a common underlying regulatory variable (see also Supplementary Information section 7).

The overall pattern of results was the same for men and women. For this reason, results are reported for both sexes combined, unless otherwise specified (see Methods).

When MPA is absent. When the MPA cue is absent—as is true whenever youngers are detecting older siblings—coresidence duration significantly predicts altruistic motivations and, separately, opposition to first and third person incest (Fig. 2). Subject's duration of coresidence with a particular sibling was positively correlated with all outcome measures: how much the subject helps that sibling (altruism: behavioural, $P = 6 \times 10^{-7}$ (or 8×10^{-7}, see Methods and Supplementary Information section 9), $N = 185$; dispositional, $P = 7 \times 10^{-6}$ (9×10^{-6}), $N = 185$); how disgusted the subject is at imagining sexual contact with that (opposite sex) sibling (sexual disgust (rank), $P = 0.0002$ (0.0003), $N = 114$; sexual disgust (Likert; men), $P = 0.0007$ (0.0009), $N = 156$, see Methods); and how morally wrong the subject judges third party sibling incest (moral opposition to incest, $P = 0.003$ (0.004), $N = 47$; see also refs 28, 29). Figure 2 shows that the effect sizes (r) for coresidence are very similar across widely divergent outcome variables, as would be expected if separate systems for altruism and sexual aversion were being regulated by the same internal variable, a kinship index.

When MPA is present. When the MPA cue is present—which can only be true for olders detecting younger siblings—levels of altruism and sexual aversion are high (Supplementary Information section 1). But in the presence of MPA, coresidence duration no longer predicts a single outcome measure (effect sizes ~0; Fig. 2; Supplementary Information section 2). Directed univariate analyses show that MPA and coresidence interact (sexual disgust (Likert; men), $P = 0.02$; sexual disgust (rank), $P = 0.003$; altruism (see Methods), $P = 0.03$; moral opposition, $P = 0.12$; see Supplementary Information section 1); the dramatic drop in effect sizes (all significant; Supplementary Information section 2) seen in Fig. 2 demonstrates that coresidence duration robustly affects altruism and sexual aversion in the absence, but not in the presence, of the MPA cue.

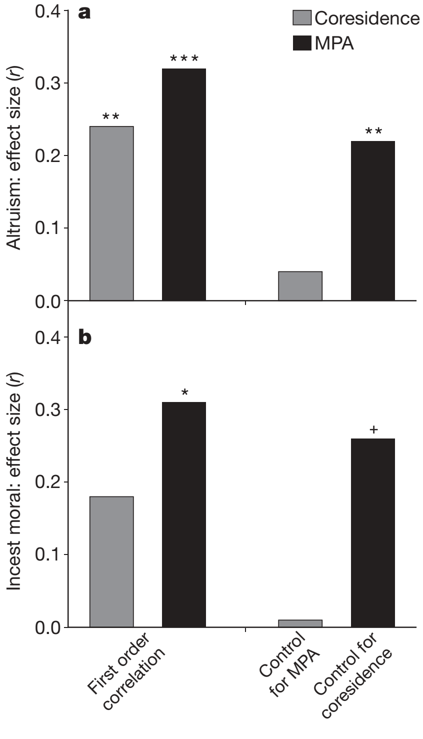

Figure 3 | When MPA and coresidence duration cues are both available, the kin detection system defaults to MPA, the more reliable cue. a, b, The only individuals for whom these cues could be jointly available are olders detecting younger siblings; each bar on the graph shows the size of the correlation between a cue and an outcome measure for this group. For olders responding to youngers, exposure to the MPA cue predicts both altruism (**a**) and moral opposition to sibling incest (**b**), and with the same effect size (black bar, first pair, each panel). The MPA cue continues to predict these disparate measures even after the effects of coresidence duration are statistically removed (black bar, second pair, each panel). In contrast, coresidence duration ceases to predict either altruism or moral opposition to sibling incest once the effects of MPA are removed (grey bar, second pair, each panel). ***$P < 0.001$, **$P < 0.01$, *$P = 0.05$, +$P < 0.10$.

MPA versus coresidence. MPA can only be observed by older siblings, and so they are the only individuals who can potentially be exposed to both MPA and coresidence duration cues. Thus analysis of olders allows one to see how the kinship estimator integrates these two cues to genetic relatedness.

Because MPA (as operationalized on these tests) is a dichotomous variable (1, 0) with 84% of older siblings scoring 1, its effects are most sensitively detected by using those outcome variables that are continuous and with high variance: altruism and moral opposition. The study assessing altruism yielded the most subject-and-younger sibling pairs ($N = 128$). As Fig. 3 shows, MPA significantly predicted altruism towards younger siblings ($r = 0.32$, $P = 0.0001$ (0.00013)), even when controlling for coresidence (partial $r = 0.22$, $P = 0.006$ (0.008), tolerance, 0.56, that is, much greater than the 0.10 collinearity threshold). This is important, because MPA and coresidence duration are themselves correlated ($r = 0.66$). In contrast, the relationship between coresidence duration and altruism towards younger siblings ($r = 0.24$) disappears when the effects of MPA are partialled out (partial $r = 0.04$, $P = 0.33$ (0.41)). When MPA, coresidence and beliefs about sibling kinship were all entered into a multiple regression, MPA was the only variable to independently predict variance in altruism towards younger siblings (partial $r = 0.27$, $P = 0.001$ (0.0013); tolerances, 0.42, 0.54 and 0.50, respectively). Moreover, MPA predicts altruism towards younger siblings better than either of its component parts (having the same mother + sibling coresidence beginning at the sibling's birth; see Supplementary Information section 3).

Although the sample size was much smaller ($N = 30$), the same MPA–coresidence pattern emerged for the moral wrongness judgments for incest (Fig. 3). For subjects with one opposite sex younger sibling, MPA predicted moral opposition at $r = 0.31$ ($P = 0.05$ (0.06)), about the same effect size as for altruism. When the effects of coresidence were statistically removed, the effect size for MPA remained virtually unchanged: $r = 0.26$. In contrast, the effect size for coresidence in predicting moral opposition was low ($r = 0.18$, $P = 0.17$ (0.21)), and when the effects of MPA were statistically removed, it disappeared entirely ($r = 0.01$, $P = 0.49$ (0.61); tolerance, 0.66).

Taken together, these analyses indicate that MPA is indeed a cue used by olders in detecting younger siblings; when MPA is present, coresidence duration is no longer used.

Alternative hypotheses

Is coresidence a kin cue or an artefact? When MPA is absent, coresidence duration correlates with altruism to the same degree regardless of the sibling's sex, as kin selection theory predicts that a cue to genetic relatedness should. But individuals are at risk for incest only from opposite sex siblings. Tellingly, moral opposition to third party sibling incest tracks duration of coresidence with an opposite sex, but not a same sex sibling ($r = -0.01$, $P = 0.47$ (0.59), $N = 30$). This pattern rules out any counter-hypothesis that coresidence duration is important not because it cues genetic relatedness, but because it is a spurious correlate of something else about the family (stability, traditional family structure, religion, and so on)[28].

The effects of coresidence when MPA is absent are also much targeted: duration of coresidence does not predict generosity outside of the sibling pair, and it is not positively correlated with moral judgments about any surveyed behaviours unrelated to incest (Supplementary Information section 4).

Early imprinting? Despite claims for an early imprinting period for sexual aversions[34,35], when MPA is absent, total duration of coresidence predicts altruism and sexual aversion better than age of sibling (or subject) when coresidence begins (start age; Supplementary Information section 5). The discovery that MPA is a potent cue for olders detecting younger sibs might explain past results suggesting an early imprinting period: start age at sibling's birth is not an independent predictor for olders detecting youngers (Supplementary Information section 3), but it is one component of the MPA cue.

Do beliefs matter? Coresidence duration predicted the outcome measures better than subjects' consciously held beliefs about siblings' genetic relatedness. Controlling for beliefs, coresidence continued to predict most outcome measures; in contrast, beliefs failed to predict most measures once the effects of coresidence were controlled for statistically (Supplementary Information section 6). Indeed, when subjects believe their sibling is step or adoptive, coresidence predicts altruism and sexual aversions, indicating that when beliefs conflict with the kin detection system, the criteria used by the kin detection system prevail (Supplementary Information section 6).

Other alternatives? Caution is always warranted in interpreting correlational findings, but it seems safe to say that altruism and sexual aversion are either regulated by the theoretically predicted cues, MPA and coresidence duration, or by unidentified cues very highly correlated with them. So far, we have been unable to find any cues that predict outcomes better than do MPA and coresidence duration.

Conclusions

The tight mesh between theoretical expectations and empirical tests provides strong support for the hypothesis that humans have a system designed by selection to detect genetic relatedness: specifically, one with (at a minimum) the computational elements outlined in Fig. 1. For example, the fact that different motivational systems are regulated in parallel by the same cues to relatedness implicates a single underlying neurocomputational variable—a kinship index—used by both. Moreover, if registered information about MPA and coresidence were fed directly into programs regulating altruism and sexual aversion, their effects would only be additive. They were not. Instead, the presence of MPA eliminated effects of coresidence. This is strong evidence for the existence of an intermediate computational device, the kinship estimator, equipped with procedures that combine these cues in a non-compensatory[40] way to compute the kinship index. These results contribute to a growing body of findings showing that humans are not immune to the evolutionary forces that have shaped other species, and that Darwinism has a central role in discovering the neural and psychological architecture of our species.

METHODS

All subjects completed a survey about family composition and attributes. For each sibling, subjects indicated that sibling's age, type of sibling (for example, biological, step), coresidence duration, age range of coresidence, and certainty of sharing the same biological mother and father[28]. From these, the following predictor variables were constructed: coresidence (duration of time a subject co-resided with his/her sibling between the subject's ages of 0 and 18); and Maternal Perinatal Association (MPA; where a score of 1 means the subject began coresidence with a sibling at the sibling's birth and is certain they share the same biological mother, and a score of 0 means any other scenario).

Instrument 1: sibling-directed altruism. Subjects ($N = 154$ (107 women); ages, 16–21, mean age ± s.d. of 18.44 ± 0.82; 287 sibling pairs) indicated the number of favours they performed for each sibling in the last month (behavioural measure), and, separately, how willing they would be to donate a kidney to their sibling (dispositional measure) on a 7-point Likert-like scale (0, not willing at all; 6, extremely willing). Responses from these measures produced the same pattern of results (Fig. 2) and were summed to produce a dependent variable, altruism (range, 0 to 16; mean ± s.d. of 7.57 ± 2.83).

Instrument 2: moral wrongness associated with third party sibling incest. Subjects ($N = 186$ (102 women); ages 18–47, mean ± s.d. of 21.54 ± 4.21) ranked 19 social transgressions on moral wrongness[28]. Two acts regarding third party sibling incest ('consensual sex between a brother and sister' and 'brother–sister marriage') were summed to produce a dependent variable, moral opposition (reverse-coded; range of 7 to 31 (mean ± s.d. of 22.43 ± 5.12)). This variable measures how morally wrong subjects view sibling incest among third parties (not incest with a particular sibling); therefore, to isolate effects to a particular sibling (in contrast to analyses in ref. 28), data analysis was restricted to individuals with only one opposite sex sibling ($N = 74$).

Instrument 3: disgust imagining sexual acts with a sibling (Likert). Subjects ($N = 455$ (264 women); ages 18–54, mean ± s.d. of 21.28 ± 3.91; a subset also completed Instruments 2 and 4) were asked how disgusting they would find engaging in various sexual and nonsexual behaviours on a 7-point Likert-like scale (0, not disgusting at all; 6, extremely disgusting). Among these were sexual acts with particular opposite sex siblings. For each opposite sex sibling, independent ratings for passionately kissing, and having sex with 'your sibling' were summed to produce a dependent variable, sexual disgust (Likert).

Initial analyses, for which non-independence was not a concern (see Supplementary Information section 8), indicated that women were at ceiling for this measure and showed significantly less variance than men in their responses (Levine's $F_{1,618} = 45.40$, $P = 4 \times 10^{-11}$). The multi response permutation procedure (MRPP)[41,42] indicated that, as predicted, women reported more disgust at sex with a sibling than did men (women (mean ± s.d.) 11.72 ± 0.98, $N = 264$; men 11.12 ± 1.96, $N = 191$; standardized test statistic of −12.72, $P = 5 \times 10^{-6}$). For this reason, this variable permitted the exploration of disgust responses in males, but not females ($N = 191$ males; ages 18–54, mean ± s.d. of 21.09 ± 3.30; 246 sibling pairs).

Sexual disgust (Likert) was transformed into a dichotomous variable: '1' was assigned if a male responded at ceiling for disgust associated with sex and kissing a sibling; '0' if otherwise (mean = 0.73, s.d. = 0.45). For the other three dependent measures, there were no sex differences in the relationships between predictor and outcome variables so results are reported for men and women together.

Instrument 4: disgust imagining sexual acts with a sibling (rank). A subset of participants who completed Instrument 3 also completed Instrument 4 ($N = 375$), which asked participants to assign a unique rank of disgust from 1 (not disgusting at all) to 50 (extremely disgusting) to eight acts, some of which involved sexual contact with a family member, short of intercourse. Using the rank of the sexual act involving a sibling, a variable, sexual disgust (rank), was constructed (women, mean = 47.36, s.d. = 3.99; men, mean = 45.51, s.d. = 9.91). To assess the effects of coresidence on sexual disgust in a way that reflects coresidence with a particular sibling, data analyses are limited to subjects with only one opposite sex sibling ($N = 243$ (144 women); ages 18–50, mean ± s.d. of 21.02 ± 2.95).

Data analyses. Correlations involving dependent measures 'moral opposition' and 'sexual disgust' controlled for the subject's sexual orientation. Controlling for social desirability yielded similar effect sizes. For univariate analyses, we used directed tests to assess predicted effects[43]. Pearson correlations for which we had prior predictions report one-tailed *P*-values, followed by directed *P*-values in parentheses (see Supplementary Information section 9). Non-independence occurs in Instruments 1 and 3 because some subjects have multiple siblings thus contributing multiple data-points. For these two studies, separate analyses using only one sibling pair per subject were carried out and yielded the same effect sizes (see Supplementary Information section 8).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Supplemental Information #1. As discussed in the text, adaptationist principles of good Bayesian design predict that the computational architecture of the kin detection system will weight the coresidence duration cue less (or not at all) when MPA—the higher quality cue—is available to the system. This predicts that outcome measures for the two motivational systems (altruism and sexual aversion) should be high when MPA is present, and that the MPA and coresidence cues will interact. As can be seen from Figure S1 and Tables S1a, b presented below, both are true.

The scatterplots shed light on the procedures the brain uses to compute the kinship index, that is, on the kinship estimator. When present, MPA produces elevated levels of all outcome measures (black lines) indicating that, upon detection, the kinship estimator translates this highly reliable cue into a variable whose magnitude represents high relatedness. In contrast, when MPA is absent and coresidence is used as a cue to relatedness, the kinship estimator appears to more slowly ratchet up the magnitude of this variable, generating a gradual increase in altruistic motivations and sexual aversions (red lines). The point at which the lines cross suggest that 14-18 years of coresidence duration for MPA absent individuals sets the kinship index to the same magnitude as for individuals with cues to MPA. Table S1b provides descriptive statistics and comparisons for each dependent measure according to whether MPA is absent or present.

The predicted interactions exist between MPA and coresidence duration for both motivational systems (altruism and sexual aversion). Interactions for three of the four outcome measures (altruism and the two sexual disgust measures) were significant (Table S1a shows that moral opposition elicited the same pattern of effect sizes as the other three measures, but had >150 fewer subjects than the other measures did; indeed, the interaction effect sizes for moral opposition and altruism are the same). Consistent with these interactions, each of the four outcome measures show significant correlations with coresidence duration when MPA is absent, but no correlation when it is present; for each measure, the drop in effect size was significant (see SI#2).

The similar pattern of data across different outcome measures indicates that both altruism and sexual aversion are regulated by a common internal regulatory variable—a kinship index. It also suggests that the kinship index is set on the basis of two distinct cues. While caution is required in interpreting any correlational research, the data show that two of the cues used are duration of coresidence and MPA—or else other cues that are highly correlated with them.

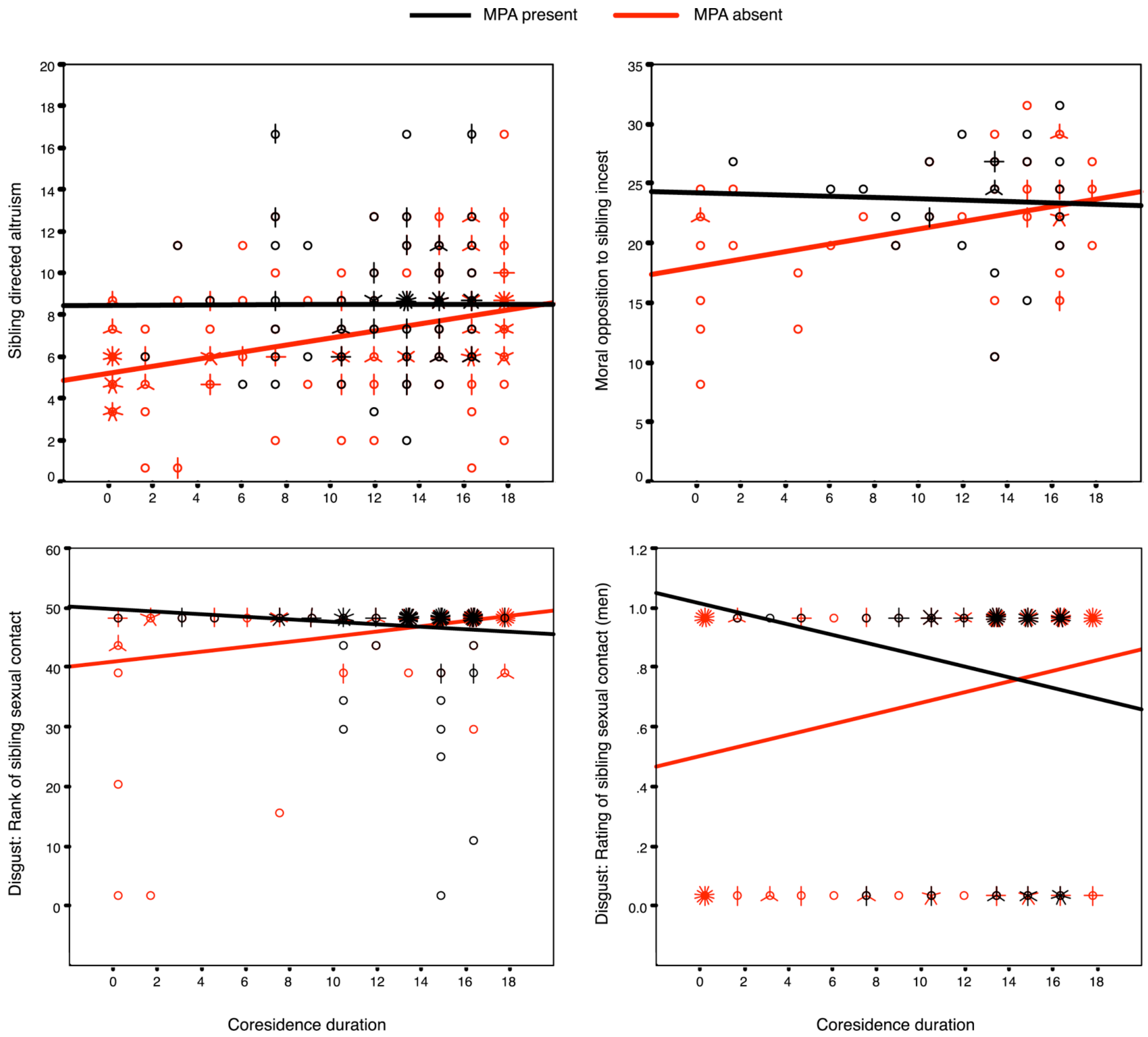

Figure S1. Interaction analysis: the effects of coresidence duration are conditional on the presence of MPA. When the MPA cue is present, levels of outcome measures are high regardless of sibling's duration of coresidence with subject (accumulated over subject's age 0-18). Accordingly, the slopes of the black lines are ~0 for all of the continuous outcome measures (sexual disgust (Likert) is dichotomous). In contrast, when the MPA cue is absent, coresidence duration is positively associated with outcome measures. The regression lines predicting outcome measures (y) as a function of duration of coresidence (x) when MPA is absent are described by the following equations (standardized beta coefficients). altruism: y = .415x; moral opposition: y = .397x; sexual disgust (rank): y = .323x; sexual disgust (Likert; men): y = .253x. Sample sizes across measures (MPA present, MPA absent): altruism (102, 185), moral opposition (27, 47), sexual disgust (rank) (129, 114), sexual disgust (Likert; men) (90, 156).

Table S1a. Interaction analysis (MPA and coresidence duration).

	Effect sizes (r) Coresidence duration (0-18) MPA Absent*	MPA Present	Univariate ANOVA (interaction between coresidence and MPA) Directed test[43], *t* statistic
Altruism (n=287)	.41	.05	1.97 (*P* = .03)
Moral opposition to incest (n=74)	.38	-.01	1.12 (*P* = .12)
Sexual disgust: Likert (n=246)	.24	-.18	2.19 (*P* = .02)
Sexual disgust: Rank (n=243)	.33	-.10	2.83 (*P* = .003)

*for *r*s, MPA absent: $.003 \leq P < 10^{-7}$ (exact values in text; composite altruism, r=.41: $P = 3\text{x}10^{-9}$ ($4\text{ x}10^{-9}$))

Table S1a shows the effect sizes between the dependent measures and coresidence duration for individuals with and without access to the MPA cue (see also Figure 2). Directed univariate tests show a significant interaction between coresidence and MPA for 3 of the 4 outcome measures. Coresidence and MPA were not highly correlated in these samples ($.10 \leq r\text{s} \leq .17$).

Table S1b. Descriptive statistics for sibling pairs with and without MPA.

	MPA absent Mean (St. Dev.)	MPA present Mean (St. Dev.)	Univariate ANOVA Directed test[43], *t* statistic
Altruism	6.97 (2.72)	8.49 (2.66)	4.58 [a]
Moral opposition to incest	21.60 (5.28)	23.59 (4.40)	1.66 [b]
Sexual disgust: Likert	.69 (.47)	.78 (.42)	1.54 [c]
Sexual disgust: Rank	46.25 (7.75)	46.92 (6.43)	0.74

[a] $P = 4\text{x}10^{-6}$; [b] *P*=.06; [c] *P*=.08

Table S1b shows that levels of outcome variables are as high or higher for sibling pairs when the MPA cue is present as when it is absent. This indicates that individuals who have not coresided for long periods can still acquire a high kinship index for a potential sibling, provided they have been exposed to their biological mother caring for that potential sibling during his/her first year of life (the MPA cue). (The MPA absent groups include individuals with low and high coresidence durations, sometimes resulting in lower means.) Sample sizes are the same as those listed in Figure S1 caption above.

Supplemental Information #2. Coresidence duration was hypothesized to drop in importance as a cue when MPA is present compared to its effects when MPA is absent—and it did (as evidenced by the significant interaction terms presented in Table S1a and as depicted in Figure 2). The dramatic drop in the coresidence effect sizes evident in Figure 2 (and Table S1a) was significant for each measure: $.0003 \leq P\text{s} \leq .053$ (altruism: Z=3.09, *P* = .001 (.0013); moral opposition: Z=1.62, *P* = .053 (.066); sexual disgust (Likert; men): Z=3.17, *P* = .0008 (.001); sexual disgust (rank): Z=3.40, *P* = .0003 (.00038). MPA present analyses: Ns=102, 27, 90, 129 for altruism, moral opposition, sexual disgust (Likert; men), and sexual disgust (rank), respectively). The small effect sizes for sexual aversion measures when MPA is present were not because some (younger) siblings might be prepubescent (thereby eliciting greater disgust and wrongness ratings, regardless of coresidence); controlling for sibling age, the relationship between coresidence and sexual aversion remains slightly negative (-.12, -.05, -.12, respectively).

Supplemental Information #3. Is MPA just a proxy for beliefs about relatedness or for coresidence having started at the sibling's birth? No. MPA predicts altruism toward younger siblings better than either of its component parts (having the same mother + sibling coresidence beginning at the sibling's birth; N = 128, stepwise multiple regression, partial *r*s: MPA *r* = .32 (*P* < .001), same mother *r* = -.09, coresidence at sibling's birth *r* = .03; the same relationship among variable holds if the regression is not stepwise).

Supplemental Information #4. The effects of coresidence are very specific: In our study, coresidence does not predict moral judgments about any behaviors unrelated to incest, it does not predict disgust associated with nonintentional sexual acts or acts involving a parent, nor does it predict non-sibling specific generosity. Each domain is discussed in turn.

Moral judgments. In the instrument assessing moral opposition, subjects were asked to rank order 19 acts in terms of how morally wrong they perceived each act to be. All acts were said to describe unknown third parties. Ranked scores were inverted such that *higher means indicate greater moral opposition.* Included in the following table are the means and standard deviations of the 19 acts for subjects with one opposite sex sibling (see Methods). Also included is the relationship of each act with coresidence duration for individuals with and without MPA. The dependent measure, moral opposition, is listed at the top of the table for comparison purposes. If the correlations found between coresidence duration and our dependent measure moral opposition for individuals with and without MPA were spurious and a result of more general processes, then other moral acts should follow the same pattern. They do not. Coresidence duration is not positively correlated with moral judgments about any behaviors unrelated to incest. Although the mother-son incest measure also correlates with sibling coresidence duration, this is likely to be a spurious correlation: Sibling coresidence correlates highly with duration of mother-subject coresidence (and far less with father-subject coresidence).

Table S4a. Moral judgments of 19 acts: descriptive statistics and effect size with coresidence duration for MPA present and MPA absent sibling pairs.

	M ± S.D.	Correlations with coresidence when: MPA$_{absent}$ N=47	MPA$_{present}$ N=27
Moral opposition (see Methods): Sex between a brother and sister (consensual) + Brother and sister marriage	22.19 ± 5.14	.38**	-.01
Individual Acts			
Molesting a child	17.48 ± 2.67	-.22	-.18
Rape	16.77 ± 2.92	-.19	-.19
A man killing his wife	14.92 ± 3.89	-.06	.05
A woman killing her husband	14.13 ± 3.49	-.15	.03
Sex between a father and daughter (consensual)	13.59 ± 3.40	.20	-.13
Sex between a mother and son (consensual)	13.00 ± 3.22	.30*	-.19
Father and daughter marriage	12.56 ± 3.17	.05	-.04
Mother and son marriage	12.52 ± 3.19	.32*	-.26
Sex between a brother and sister (consensual)	**11.53 ± 3.08**	**.27***	**-.19**
Brother and sister marriage	**10.65 ± 3.01**	**.39****	**.16**
Assault with a weapon	10.41 ± 2.94	-.11	.06
Robbing a bank	8.19 ± 3.11	-.16	.32
Selling cocaine	7.53 ± 3.58	-.17	.02
Breaking and entering	7.03 ± 2.80	-.00	.15
Embezzlement	6.67 ± 2.88	-.24	.06
Smuggling illegal aliens into the country	5.28 ± 2.68	.15	.05
Public drunkenness	3.23 ± 2.55	-.20	.24
Speeding on the highway	2.60 ± 2.97	-.02	.05
Smoking marijuana	2.29 ± 2.17	-.32*	.05

*p ≤ .05 (two-tailed); **p ≤ .01 (two-tailed)

Sexual disgust (rank). Subjects were asked to rank eight items on a scale of 0 (not disgusting at all) to 50 (extremely disgusting). These items included sexual contact with a parent and sibling short of sexual intercourse. They also included unintentional acts to test separate hypotheses regarding intentionality. As the following table shows, for individuals without MPA, coresidence predicts only the disgust associated with the intentional sibling sexual act; disgust associated with unintentional acts and those involving a parent did not correlate with sibling coresidence duration for individuals with MPA absent.

Table S4b. Rank of sexual act involving a sibling: descriptive statistics and effect size with coresidence duration for MPA present and MPA absent sibling pairs.

	M ± S.D.	Correlations with coresidence when: MPA$_{absent}$ N=109	MPA$_{present}$ N=124^{+}
Individual Acts			
Parent fondling you$^{\Psi}$	48.44 ± 5.21	.00	.01
Sibling fondling you$^{\Psi}$	**46.60 ± 7.07**	**.29*****	**-.10**
Parent intentionally laying on top of you	40.47 ± 13.04	-.09	-.02
Sibling intentionally laying on top of you	35.07 ± 15.90	.12	-.05
Parent unintentionally touches you$^{\Psi}$	20.78 ± 16.21	.03	.01
Sibling unintentionally touches you$^{\Psi}$	19.62 ± 16.11	.08	.02
Parent trips on shoes and falls on you	16.96 ± 16.16	-.06	-.14
Sibling trips on shoes and falls on you	14.81 ± 15.21	-.02	-.14

***p = .001; $^{+}$data include all subjects who ranked all eight items. $^{\Psi}$ Item was about brother or father for female subjects; sister or mother for male subjects. Unintentional touches were to same body areas as fondling item.

Altruism. An alternate explanation of our findings is that there exist stable differences in general altruism between individuals with and without MPA and that coresidence duration somehow tracks this difference. If this were the case, the pattern of effects found between coresidence duration and kin-directed altruism for individuals with and without MPA should hold for more general, non-sibling related altruism. Our dataset allowed us to test this alternate hypothesis. In the Altruism instrument, subjects were asked two questions regarding their overall altruistic tendencies: “How generous would you consider yourself to be compared to your peers?” and “How generous would your peers consider you to be?” If *all* altruistic motivations are affected by MPA presence versus absence (or something particular to older versus younger siblings in general), then coresidence duration should predict these other indices of altruism in the same way they predict sibling directed altruism. They do not. Whereas coresidence duration with a sibling for whom MPA was absent predicts behavioral and dispositional measures of altruism directed toward that sibling (for combined altruism measure: $r = .41$, $P = 3\text{x}10^{-9}$ ($4\text{ x}10^{-9}$), N = 185), it does not predict altruism as indexed by either generosity question (rs = .00, .01, Ps $\geq$ .43 (.54)). Similarly, coresidence duration does not predict either generosity question when MPA is present ($r = .046$, $P = .37$ (.46); $r = .07$, $P = .31$ (.39), respectively).

Supplemental Information #5: Start age.

When MPA is absent, the sibling's age when coresidence with the subject begins is highly correlated with total duration of coresidence from subject's ages 0-18 (rs ~ -.70; tolerances: .48-.57). When sibling's start age is controlled for, coresidence continues to significantly predict three out of four outcome variables: moral opposition (*partial* r = .26, P = .05 (.06)), altruism (*partial* r = .25, P = .0003 (.0004)), and sexual disgust (Likert; men) (*partial* r = .17, P = .018 (.023)). (Sexual disgust (rank) *partial* r = .10, P = .16 (.20)). In contrast, when coresidence is controlled for, sibling's start age fails to predict three out of four measures (*partial* rs ~0; .14 < Ps < .48 (.18-.60); only sexual disgust (rank) yielded a significant *partial* r = -.26, P = .003 (.004), N=111).

Distinguishing the *subject's* start age from total duration of coresidence is more difficult because, among people with MPA absent, subject's start age is even more highly correlated with coresidence duration than is sibling's start age (-.79 ≤ rs ≤ -.92). Like sibling's start age, subject's start age fails to predict the same three outcome variables once coresidence is controlled for (moral opposition: *partial* r = -.14, P = .17 (.21), tolerance=.16; altruism: *partial* r = .11, P = .08 (.10), tolerance=.29; sexual disgust (Likert; men): *partial* r = .06, P = .25 (.31), tolerance=.20; only sexual disgust (rank) remained significant: *partial* r = -.19, P = .03 (.04), tolerance=.38). In contrast, total duration of coresidence continued to predict altruism (*partial* r = .32, P = $4\text{x}10^{-6}$ ($5\text{x}10^{-6}$)) and sexual disgust (Likert; men) (*partial* r = .16, P = .025 (.03)), even after controlling for subject's start age. Nevertheless, definitively distinguishing subject's start age from total coresidence duration for MPA absent individuals will require a sample in which they are not as highly correlated.

For MPA present individuals, subject's start age is not correlated with any outcome measure: altruism: r = .08, P = .21 (.26), N=102; moral opposition: r = .08, P = .35 (.44), N=26; sexual disgust (Likert; men): r = .11, P = .18 (.23), N=77; sexual disgust (rank): r = .09, P = .16 (.20), N=129.

Supplemental Information #6. Effects of beliefs.

MPA absent. Most individuals for whom MPA is absent are youngers detecting older sibs (≥88%), but a minority are olders detecting younger sibs. Olders not exposed to the MPA cue present a different profile from youngers, demographically, theoretically, and in dependent measures, in a way suggesting that being older than one's sibling may itself be a cue with probative value that the kin detection system is designed to use: The younger sibling of an older individual with MPA absent is almost always a step or paternal half sibling (indeed, the average degree of kinship for MPA absent olders is far lower than for MPA absent youngers (.14 versus .38, $P < .001$, and the sibling age discrepancy is much larger for MPA absent olders than for youngers). Unfortunately, the demographics and responses for the two MPA absent groups differ in ways that confound attempts to assess how similar they are (for each measure, there are too few MPA absent olders to draw reliable inferences). Thus the more conservative route was to restrict MPA absent analyses about beliefs to the large sample of youngers with older siblings, for whom reliable tests can be conducted (see also SI#7).

For youngers detecting olders, do beliefs matter? The subjects' consciously held beliefs about a sibling's degree of kinship (i.e., whether the subject reports the sib was full, half, or step/adoptive) are highly correlated with duration of coresidence with that sibling (across studies: .64 - .71). Nevertheless, coresidence duration predicted the outcome measures better than subjects' consciously held beliefs about their degree of relatedness. Controlling for beliefs, coresidence duration continues to significantly predict all three sexual aversion measures (partial *r*s: moral opposition: $r = .33$, $P = .02$ (.025), N=38; sexual disgust (rank): $r = .25$, $P = .005$ (.006), N=103); sexual disgust (Likert; men): $r = .17$, $P = .03$ (.04), N=131) and marginally predicts altruism ($r = .12$, $P = .06$ (.075), N=162). In contrast, when coresidence is controlled for, the subject's beliefs about kinship fail to correlate with any of the three sexual aversion measures (*partial r*s -.16, .08, .08, ns); only altruism shows an effect of belief independent of coresidence for this group of subjects (*partial* r=.29, $P = 9\text{x}10^{-5}$ (10^{-4})).

A critical test about the power of beliefs can be constructed by seeing what happens when explicit beliefs about kinship are pitted against a conflicting output from the kin detection system. This test can be conducted using subjects with older step and adoptive siblings: these subjects believe their siblings are not biologically related to them, yet are in a group where coresidence should matter (given the model proposed). Two samples yielded enough subject-and-older step/adoptive sibling pairs to conduct an analysis. When subjects believe their siblings are not blood kin, coresidence still robustly correlates with altruism toward that sibling and disgust at imagining sexual contact with that sibling (altruism: $r = .38$, $P = .04$ (.05), N = 22; sexual disgust (Likert; men): $r = .47$, $P = .03$ (.038), N = 16. Sexual disgust (rank) has only 8 relevant sib pairs; $r = .22$). (Similar effect sizes are found for the small sample of olders with younger step/adoptive siblings (altruism $r = .43$ (N=7, $P = .16$ (.20)); sexual disgust (Likert; men) $r = .40$ (N = 11, $P = .13$ (.16); the other measures had only 2 and 4 relevant pairs)). In short, when subjects believe their elder sibling is step or adoptive, *coresidence trumps beliefs about kinship*, indicating that when beliefs conflict with the kin detection system, the criteria used by the kin detection system prevail.

For olders detecting younger siblings, do beliefs matter? Beliefs about a younger sibling's degree of kinship did not significantly correlate with three of the four outcome variables (.11 < *r*s < .15); it correlated only with sexual disgust (rank) ($r = .18$, $P = .016$ (.02)).

It is perhaps worth noting that, for populations like ours, reported kinship reflects genetic kinship in 95-98% of cases.[44,45] Thus the beliefs variable indexes both genetic relatedness and subjects' beliefs about it.

Supplemental Information #7. A pattern similar to that shown in Figure 2 (see text) emerges if we compute the effects of coresidence for younger subjects detecting older siblings versus older subjects detecting younger siblings (instead of for MPA absent versus MPA present, as in Fig 2). Figure S7 presents this different way of organizing the data, showing that, as predicted, relatedness is computed differently for older versus younger siblings. Coresidence duration significantly predicts altruism and sexual aversion measures for youngers detecting olders. In contrast, for olders detecting youngers, coresidence fails to significantly predict any of the sexual aversion measures. Coresidence continues to predict altruism (although not once MPA has been controlled for, see Fig. 3), but the effect size is significantly lower than that found for youngers detecting olders.

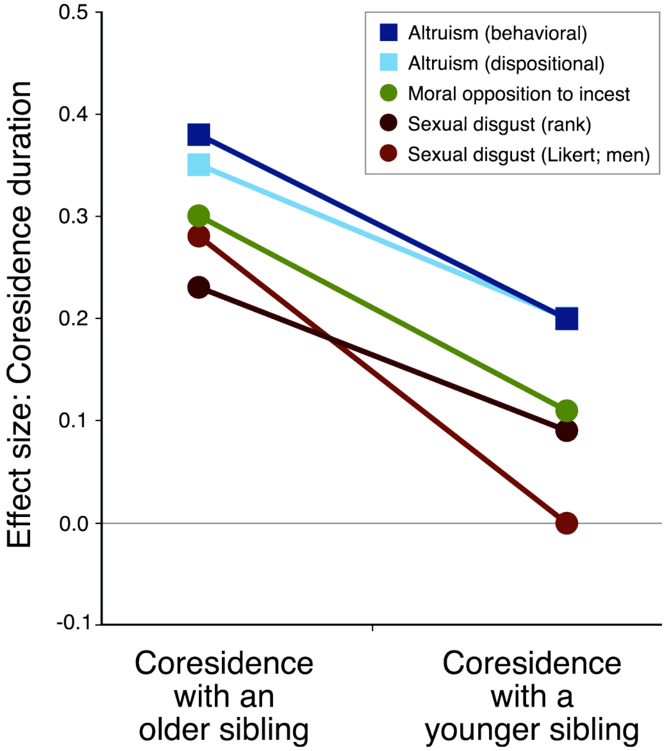

Figure S7. Coresidence duration effect sizes as a function of whether the subject is younger or older than his or her sibling.

Supplemental Information #8. For two instruments, altruism and sexual disgust (Likert; men), some subjects had more than one sibling; these subjects generate >1 data point (one for each subject-sibling pair). This raises a question of independence (though one that works against our hypothesis; any subject variable that predicts similarly for multiple subject-sibling pairs will tend to reduce the effects of coresidence). To address the independence issue, additional analyses were conducted for those instruments that collected information for more than one sibling pair per subject. (Moral opposition and sexual disgust (rank) only considered subjects with one opposite sex sibling, thus posing no problems of non-independence.) The following table displays the effect sizes between coresidence and the dependent measures for individuals with and without MPA for two samples: (i) all sibling pairs (as reported in the main text) and, (ii) for one randomly chosen sibling pair per subject (in parentheses). As data analyses show, when only one sibling pair is chosen per subject, the effect sizes remain unchanged.

Table S8. Non-independence: comparison of all sibling pairs and one sibling pair per subject

	MPA absent All sibling pairs* (one pair per subject)	**MPA present** All sibling pairs (one pair per subject)
Altruism N=287 (N=154)		
Composite	.41 (.43[a])	.00 (.18)
Behavioral	.34 (.34[b])	-.01 (.15)
Dispositional	.30 (.36[c])	.05 (.16)
	N=185 (N=103)	N=102 (N=51)
Sexual disgust (Likert; men)	.24 (.27[d])	-.18 (-.17)
N=246 (N=191)	N=156 (N=116)	N=90 (N=75)

* exact P values in text. [a]$P=10^{-6}$; [b]$P=10^{-4}$; [c]$P=10^{-5}$; [d]$P=10^{-3}$ (for directed *P* values, multiply by 1.25)

Supplemental Information #9. One-tailed versus directed tests. In the text, we report *P* values for both one-tailed and directed tests, because each has strengths the other lacks. One-tailed tests were designed to powerfully test *a priori* predictions about the direction of a relationship (e.g., that two variables will be positively correlated). They are particularly appropriate where one is testing a series of predictions tightly derived from a highly constrained prior theory (which is the case for most of our analyses.) If a relationship *does* occur in the direction opposite from that predicted, one rejects the hypothesis that there is a relationship in the predicted direction; however, the one-tailed test provides no measure of whether the *unpredicted* relationship is significant or just noise. (In the studies reported herein, we found no relationships in a direction opposite from that predicted.)

To address this problem, Rice and Gaines (1994) suggest using 'directed' tests as opposed to 'one-sided' tests. Directed tests allocate .04 of a total alpha of .05 to the predicted tail and .01 to the unpredicted tail, leaving open the possibility of finding a significant effect in the non-predicted direction. (This is achieved at the cost of lower power for finding predicted effects.) For those interested in what the results would be using directed tests, these are reported in parentheses after the one-tailed *P* values, in the form "(*P* = one-tailed (directed))". For the predicted tail, directed *P* = one-tailed *P* x 1.25).

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